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Visual, Chemical and Sound Stimuli as Cues in the Sex Discriminatory Behavior of the Gobiid Fish *Bathygobius soporator*

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(Plate I)

INTRODUCTION

SEX discrimination, in its broad sense, may be defined as a pattern of activity exhibited by one animal toward another of the same species, which activity varies according to the sex, maturity and stage of gonadal cycle of the other. The probability of successful pairing and reproduction is thus increased. Such behavior can also maintain a pair until both members attain the physiological condition necessary to consummate mating. Indeed, the behavior pattern itself can stimulate and synchronize the achievement of this physiological state.

Among fishes, the territorial and nesting species are particularly useful in studies of sex discrimination, since the behavior of a territory-holding male is well differentiated with respect to intrusion by females and other males. Such sexually dimorphic behavior (as well as structure, coloration, etc.) is present in the Centrarchidae (Noble, 1934; Breder, 1936), some of the Cichlidae (Breder, 1934; Noble & Curtis, 1939), Gobiidae (Guitel, 1892, 1895; Tavolga, 1954), Blenniidae (Guitel, 1893; Breder, 1939, 1941), and numerous other groups of teleosts. Among some species, the behavior of the two sexes is differentiated to a lower degree, and the distinctions between male and female activity may be entirely quantitative, as in the cichlid fish *Tilapia macrocephala* (Aronson, 1949).

Two behavior patterns are commonly observed among territorial fishes (and in many other animals as well). On the one hand the encounters between a territory-holding male and an intruding male consist of color flashing, nipping or pecking, and the display of similar identifying devices. Terms such as "fighting," "combat," "territorial aggression," "intimidat-

ing" or "warning" devices, have been commonly employed in descriptions of this behavior. Morris (1954), and others, have used the term "agonistic behavior" for this and all other activities not directly associated with mating. On the other hand, there is the activity of a male which attracts and stimulates a female toward eventual mating. "Courtship" is the almost universally used term for this behavior. The two behavior patterns are not mutually exclusive, however, and one frequently contains many of the elements of the other. Thus, a given component act can lead to very different results depending upon the context within which the movement occurs. The terms "courtship" and "combat," as used by some authors, frequently imply the presence of two separate neural mechanisms, centers or drives. As used in this report, however, these terms describe two patterns of behavior which occur as part of the general reproductive activity, and the emphasis here is upon the external stimuli which control the direction of response.

The majority of analytical studies on fish behavior have been concerned only with the visual cues which lead to sex discrimination, and within these investigations various areas of visual perception have been included, i.e. shape, shade, color and movement. Artificial models have been used in the work of ter Pelkwijk & Tinbergen (1937) and Tinbergen & Van Iersel (1947) on the stickleback *(Gasterosteus)*, and by Baerends & Baerends-Van Roon (1950) on the Cichlidae. Most of these studies were done within the theoretical framework of the releaser hypothesis of innate behavior (Baerends, 1950; Lorenz, 1950; Tinbergen, 1951).

Other sensory mechanisms have been only infrequently investigated in connection with reproductive behavior. The role of tactile and chemical factors was described in the courtship

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behavior of the catfish *(Ameiurus)* by Breder (1935), and the blind goby *(Typhlogobius)* by MacGinitie (1939). Sounds produced by the purring gourami *(Ctenops vittatus)* are known to form a part of the pre-spawning behavior pattern (Stampehl, 1931). It is conceivable, then, following the general view of Lashley (1938), that a number of sense modalities may be simultaneously responsible in eliciting and modulating the sex discriminatory behavior among teleosts.

Males of the gobiid species, *Bathygobius soporator* (Cuvier & Valenciennes), possess a highly differentiated behavior pattern, particularly during their territorial and pre-spawning activities (Tavolga, 1954, 1955a). In addition to visual cues, chemical and sound stimuli were found to elicit and orient the behavior of both males and females. The following report presents data on the role of these factors in the pre-spawning behavior pattern.

Acknowledgements

Source and Maintenance of Material

The specimens of *B. soporator* were collected from tide pools and shallows along the Intracoastal Waterway, in the vicinity of Marineland, Florida. All the collections and observations were made during the summer months, when the spawning season of this species is at its height.

Individuals used here were all sexually mature and varied in size from 40 mm. to 90 mm. in standard length. The males which were used as test animals in the observations were chosen from the largest size group, ranging from 80 mm. to 90 mm. Females ranged in size from 40 mm. to 75 mm. Some smaller males, below 75 mm. in length, were also used.

Large males were isolated in five-gallon aquaria, and the rest were kept as stock (sexes separate) in ten-gallon tanks. All aquaria were supplied with running, filtered sea water, and the animals were fed daily on minced shrimp and mullet.

The resident males were provided with shelters consisting of unglazed flooring tiles (approximately 4″×4″×½″), one of which was inclined against the front glass of the aquarium. These triangular shelters were readily used by the gobies for hiding and spawning.

Summary of Reproductive Behavior Pattern

The reproductive behavior in *Bathygobius* has been reported in detail elsewhere (Tavolga, 1954, 1955a), but a brief summary is appropriate here.

The male enters a shell or crevice and establishes a territory in the vicinity, and cleans loose sand from the interior of the shelter. Other males intruding into the territory are chased or fought. The combat behavior between males is characterized by a sideward approach and an intense darkening of the coloration, accompanied by fin erection, gaping, quivering, butting, tail slapping and biting. Much of this type of behavior is included within the term "lateral display" as described by Baerends & Baerends-Van Roon (1950) for the Cichlidae.

In the presence of a gravid or pre-gravid female, the coloration of the resident male changes to a light, patternless tan with a blackened chin and throat. The female is approached with rapid fanning and gasping movements. If ovulation is imminent, the gravid female follows the male into the shelter and there deposits adherent eggs on the inner surfaces. After spawning, the male guards and fans the eggs until they hatch four to five days later.

It must be emphasized that although in summary the pattern may appear sterotyped, numerous variations of both qualitative and quantitative nature occur (Tavolga, 1955a).

OBSERVATIONS

Analysis of Visual Stimuli

Twenty mature male *Bathygobius* were isolated in small 5-gallon tanks with shelters for three days prior to testing. The tests were made once a day, thus allowing sufficient time to elapse between tests to reduce the amount of overlap of responses (Tavolga, 1955a). In the majority of the tests, the stimulus-animal was placed in a one-liter Erlenmeyer flask filled with sea water, and the flask was slowly lowered into the tank. The actions of the resident male were observed for a five-minute period, the flask removed and then dipped into the next tank. One side of each tank was constructed of slate (containing an overflow); thus the resident was

unable to see into neighboring aquaria. In some of the tests, the stimulus-animal was confined in a screw-top vial, filled with sea water, into which the fish fitted tightly. The vial was lowered into each tank on a thread. In these tests, the stimulus-animal was unable to make any movements other than sporadic respiratory ones. In another series of tests, the stimulus-animals were anesthetized in 0.08% MS-222 (Tricaine methanesulfonate — Sandoz Pharmaceuticals) dissolved in sea water. This concentration stopped all except slow opercular and pectoral fin movements. The anesthetic induced an expansion of all melanophores, thus presenting a totally blackened stimulus-animal. In contrast, some of the stimulus-animals were injected with 0.05 ml. of 1/1000 adrenalin (Parke-Davis) in normal saline. This drug induced a contraction of melanophores and the animals became a light tan color with slight evidences of crossbands. The adrenalin-treated fishes were quiescent and exhibited no more movement during the tests than did the anesthetized animals. These drugged fishes were placed in a flask and used as stimulus-animals as described above.

In most cases, non-anesthetized stimulus-animals exhibited little movement other than respiratory and pectoral fin pulsations, and certainly no reactions which could be correlated with the behavior of the resident. In some cases, notably among males, the stimulus-animals exhibited combat behavior shortly after the initial reaction of the resident.

The stimulus-animals were all closely matched as to size, ranging from 60 to 65 mm. in standard length. In test series I, four types of stimulus-animals were used as follows:

(a). Gravid females—mature eggs easily extrusible; abdomen distinctly swollen.

(b). Non-gravid females — eggs not extrusible; abdomen flat as in males.

(c). Non-gravid females — eggs not extrusible; recently fed so that abdomen is swollen to same extent as in gravid females.

(d). Males—young, but sexually mature.

The type of stimulus-animal was alternated from day to day (as shown in Table 1). Each resident male was tested on 20 successive days, making 400 tests in all. The instances in which the stimulus-animals exhibited combat behavior are marked with an asterisk in the table. The symbols indicate the type of reaction by the resident male, as described below.

In all cases, the resident males approached the stimulus-animal within a few seconds. The types of reactions were classified and roughly quantified as follows:

C4—An immediate change to courtship coloration accompanied by courtship movements, followed by an approach to the stimulus-animal and continuation of the courting for the full five-minute test period.

C3—Initially an approach to the stimulus-animal, followed by courtship for the full test period.

C2—A vigorous courtship beginning immediately after the approach; courtship continued for less than one minute; male then became quiescent and often returned to the shelter.

C1—A slight lightening of the coloration shortly after the approach; no courtship movements, followed by return to shelter.

N—An approach to the stimulus-animal; no color change; quiescence or return to shelter within less than 30 seconds.

F1—An approach accompanied or followed by a slight darkening of the coloration; no actual combat; shortly followed by quiescence or return to the shelter.

F2—An approach followed by a definite darkening toward the combat coloration; some combat movements and sideward approaches which last for not more than one or two minutes.

F3—An approach followed by a complete exhibition of the combat coloration and behavior; continued for full test period.

F4—Darkening to combat coloration, followed by approach to stimulus-animal; combat behavior continued for full test period.

Table 1 shows that in some cases the behavior of the resident began as courtship but subsequently changed to combat. In all such cases, the stimulus-animal exhibited darkening and sideward approach. In one instance, the response changed from a darkened combat type (F1) to a lightened coloration of incipient courtship.

On the basis of the observations listed in Table 1, it is apparent that the types of reactions of the resident males were not correlated with the sex or gravidity of the stimulus-animals, except in the cases where the stimulus-animals exhibited combat behavior. Males nos. 1 and 16 reacted with courtship toward all stimulus-animals; males nos. 2, 11 and 15 courted in all cases, except where the introduced animals showed combat, in which tests the residents' behavior shifted toward the combat type. Males nos. 10, 12, 18, 19 and 20 showed frequent combat type responses, mixed with some C and N reactions. The remainder gave variable responses, consistent only in that frequent neutral and weak responses were observed.

Series II (Table 2) represents a continuation of the tests in series I, using the same resident

TABLE 1. RESPONSES OF RESIDENT MALES TO VISUAL STIMULUS OF GOBY IN FLASK (TEST SERIES 1).

Type of Stimulus-animal in Flask	Resident Males & Their Responses																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Female—gravid	C4	C4	N	N	C1	C4	F1	F1	F4	C2	C4	F1	N	F1	C4	C4	C3	N	C2	C1
Female—gravid	C4	C4	N	N	C1	C4	F1	C1	N	C2	C3	F1	C1	C1	C4	C4	C2	F1	C3	C3
Female—non-gravid (fat)	C4	C3	N	N	C1	C3	C1	C1	N	C2	C4	F1	C1	C2	C4	C3	C2	N	C2	C2
Female—non-gravid (thin)	C4	C3	F1	C2	C2	C3	C1	C1	N	C2	C3	F1	N	C1	C4	C3	C3	N	C1	C2
Male	C4	C3	F1	C1	C2	C3	C1	C1	C1	C3	C4	N	N	N	C4	C4	C2	F3*	C1- / F3*	C2- / F3*
Male	C4*	C2- / N*	F3*	C1- / F3*	C1- / F3*	C4- / F3*	C1- / F3*	C1- / F3*	F3*	C1- / F3*	C1- / F3*	F3*	F3*	F3*	C2- / F3*	C4*	C2- / F3*	F3*	F3*	F3*
Female—gravid	C4	C3	F1	F1	C1	C3	F1- / C2	C1	F1	F1	C4	F1	F1	N	C3	C4	N	F3	F1	N
Female—non-gravid (thin)	C4	C3	F3*	F3*	C1	C3	N	C2	N	C1	C4	F1	F3*	N	C3	C4	N	F3*	F3*	N*
Female—non-gravid (thin)	C4	C3	F1	F1	C2	C2	C1	C2	N	C1	C4	F1- / C2	F1	C1	C3	C4	N	F2	F3	F1
Female—non-gravid (fat)	C4	C3	N	C1	C1	C2	C1	C1	C1	C1	C4	F1	N	N	C3	C4	C1	F2	F2	F2
Female—gravid	C4	C3	N	N	N	C2	N	N	C2	C1	C4	F1	N	C1	C3	C4	C1	F1	F2	F3
Male	C4	C3	N	F3*	N	C1	F3*	N	C2	F3*	C4	F3*	N	C1	C3	C4	C1	F3*	F3*	F3*
Female—gravid	C4	C4	N	N	N	C2	F2	N	C1	F4	C4	F3	N	C1	C3	C4	N	F1	N	F3
Male	C4	C3	N	C1	N	C2	F2	N	C1	F4	C4	F3	F1	C1	C3	C4	N	F2	F2	F4
Female—non-gravid (thin)	C4	C4	F1	C1	N	C2	F1	N	C2	F4	C3	F3	F1	C1	C3	C4	N	F2	F2	F4
Female—non-gravid (thin)	C4	C4	N	C1	N	C2	F1	N	C2	F3	C3	F2	F1	C1	C3	C4	N	F3*	F3*	F4*
Female—gravid	C4	C4	C1	C1	C1	C2	N	C1	N	F1	C3	F2	F2	N	C3	C4	C1	F2	F1	F3
Female—gravid	C4	C3	C1	N	C1	N	C1	C1	C1	N	C3	F1	F1	C1	C3	C4	C1	F1	F1	F2
Male	C4*	C2- / F3*	C1- / F3*	F3*	F3*	F2*	F2*	F3*	F3*	F3*	C2- / N*	F3*	F3*	F3*	C2- / F3*	C4*	C2- / F3*	F3*	F3*	F3*
Female—gravid	C4	C3	C1	C1	N	F1	F1	N	N	N	C3	F1	N	N	C3	C4	C3	N	F1	F3

* Cases in which stimulus-animal exhibited combat behavior.

males. The first five tests used stimulus-animals that were immobilized in small vials. The rest of the tests used anesthetized and adrenalin-treated males. Table 2 shows that in this series, as before, males nos. 1, 2, 11 and 15 gave strong courtship responses. No. 17 gave stronger courtship responses here than in series I. No. 16 also showed strong courtship, but on the 15th test, and those following, changed to a neutral reaction type. Males nos. 6, 7, 10, 18 and 20 exhibited frequent combat responses. The remainder gave weak and neutral reactions. In some cases, there appeared to be a correlation of the reaction type with the coloration of the stimulus-animal, i.e. nos. 6 and 18 showed combat more consistently towards the dark anesthetized animals.

In comparing the two series, disregarding differences in the types of stimulus-animals, some of the males remained consistent in their responses. Some, however, changed their predominant response types, viz. nos. 6, 10, 17 and 18.

Test series III was set up to determine if the predominant response types of resident males could be altered by a strong combat or courtship experience. The same resident males were used as in series I and II. A large mature male was introduced into the aquaria of half of the residents—nos. 1, 2, 3, 8, 11, 12, 14, 15, 16 and 17. In each case, mutual combat began within a few seconds and was allowed to continue for one or two hours. In two instances, the introduced animal had to be removed in slightly less than an hour when it became evident that the resident would inflict serious damage. Gravid females were placed with resident males nos. 4, 5, 6, 7, 9, 10, 13, 18, 19 and 20. Courtship began immediately, and was permitted to continue for two hours.

Half an hour after the introduced animals were removed, the residents were tested in their reactions toward anesthetized and adrenalin-treated males confined in a flask (as in series II), and thereafter the tests were repeated nine additional times at daily intervals. Half these tests (resident nos. 1-10) used adrenalin-treated stimulus-animals, the remainder (resident nos. 11-20) used the darkened MS-222-treated animals.

Table 3 shows that the combat or courtship experience persisted in its effect on the first and, in many cases, subsequent tests. Males nos. 1, 2, 11, 15, 16 and 17 were, in series I and II, strong in their courtship responses, and the combat experience changed their subsequent responses to combat or neutral types. Nos. 8 and 14, after previous neutral responses (in series II), changed to strong combat reactions as a result of the extended combat experience.

Nos. 3 and 12 appeared to be only slightly, if at all, affected by the combat experience.

Seven of the ten males given a courtship experience persisted in strong courtship responses in subsequent tests. This change to courtship was particularly striking in nos. 7, 10 and 18, which showed frequent combat responses in previous series. Nos. 6, 19 and 20 exhibited only a brief change to courtship response as a result of the courtship experience.

The observations summarized in Table 3 do not indicate any correlation between the responses of the residents and the color phase of the stimulus-animals.

Series IV comprises a group of miscellaneous visual stimulus tests that were performed on resident males other than the 20 used in series I-III.

In three instances, males that were brooding eggs were given the visual stimulus tests. In no case were any courtship responses observed, and, in 8 out of 9 tests, combat took place.

In preliminary tests with stimulus-animals in a flask, it was found that courtship-oriented residents reacted toward very small stimulus-animals. For example, a 25 mm. goby in a flask elicited a strong courtship response from a 75 mm. resident male. This same stimulus-animal without the protection of a flask would otherwise be chased about and even nipped to death in a few minutes by the male. Stimulus-animals below this size elicited a courtship response only in combination with olfactory stimuli, as will be described later.

Attempts to elicit courtship responses with simplified models were uniformly unsuccessful. Similarly, no courtship or combat responses could be elicited using dead or anesthetized gobies manipulated with threads or wire. It appeared that the reactions of the residents to these and to the models were similar. In most cases, the resident darted out of his shelter toward the stimulus object, and immediately returned to the shelter. In several tests, the residents nipped at the dead gobies as they would at a piece of food.

Other species of fish were used in flasks as test objects, e.g. gobies (Gobiosoma bosci and Gobionellus boleosoma), blennies (Hypsoblennius ionthas and Hypleurochilus geminatus), and others (Fundulus heteroclitus and Mugil cephalus). The specimens used were selected to fall into the size range 60-65 mm. In a few cases, the resident males showed a few quick approaches, but most of the time the stimulus-animal was not reacted to in any way.

Demonstration and Analysis of Chemical Stimulus

The initial demonstration of a chemical stimu-

TABLE 2. RESPONSES OF RESIDENT MALES TO VISUAL STIMULI (TEST SERIES II).

Type of Stimulus-animal	Resident Males & Their Responses																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
(Immobilized in vial)																				
Female—gravid	C4	C2	N	C1	C1	N	N	N	C1	F2	C3	N	N	C1	C3	C4	C3	F1	F1	F1
Female—non-gravid (fat)	C4	C2	N	C1	C1	N	N	N	C1	F2	C3	N	F1	C2	C4	C4	C3	F3	F1	N
Female—non-gravid (thin)	C4	C3	C1	C2	N	F1	N	N	N	F2	C3	N	F1	C3	C4	C3	C3	F2	N	N
Male	C4	C2	C1	C3	N	F1	F1	N	C1	F2	C3	N	N	C1	C3	C4	C4	F2	N	N
Female—gravid	C4	C3	C1	C2	C1	F1	F1	N	C1	F2	C3	N	N	N	C3	C4	C4	F2	N	N
(Drugged males in flask)																				
Adrenalin	C4	C3	N	C1	C1	F1	F1	C1	N	F2	C3	N	N	C3	C3	C4	C4	F3	F2	F4
MS-222	C4	C3	N	N	C1	F2	F1	N	N	F2	C2	F2	N	N	C3	C4	C4	F3	F2	F4
Adrenalin	C4	C4	N	N	C2	N	F1	N	N	F2	C2	N	F1	N	C3	C3	C4	F3	F2	F3
MS-222	C4	C3	C1	C1	C1	F2	F1	N	N	F2	C3	F2	F1	N	C4	C4	C4	F4	F2	N
Adrenalin	C4	C3	C1	C1	C1	N	F1	N	C1	F2	C3	N	F1	C1	C4	C4	C4	F4	F1	N
MS-222	C4	C2	F1	F1	N	F2	F2	N	C1	F3	C4	N	F2	C1	C4	C4	C4	F4	F2	N
Adrenalin	C4	C3	C1	C1	N	N	F1	N	C1	F2	C4	N	N	C1	C3	C4	C4	F1	F1	N
MS-222	C4	C2	C1	N	N	F2	F3	N	N	F3	C4	N	N	C1	C3	C4	C4	F4	N	F2
Adrenalin	C4	C3	N	N	N	N	F1	N	N	N	C2	F3	N	N	C3	N	C4	F1	N	F2
MS-222	C4	C3	N	F1	N	F2	F3	N	F1	F3	C3	N	N	N	C3	N	C4	F4	N	F1
Adrenalin	C4	C3	N	N	F1	N	N	N	N	N	C3	F2	N	C1	C3	N	C4	F1	N	F1
MS-222	C4	C2	N	N	N	F2	N	N	F1	N	N	F1	N	N	C3	N	C4	F4	F1	F2
Adrenalin	C4	C3	N	F1	N	N	F1	N	F1	N	C3	F1	N	C1	C4	N	C4	F1	N	N
MS-222	C4	C3	N	N	N	F2	F1	N	F1	N	C3	F1	N	N	C3	N	C4	F4	N	N

TABLE 3. EFFECTS OF PRIOR EXPERIENCE UPON RESPONSES OF RESIDENT MALES TO VISUAL STIMULUS (TEST SERIES III).

	Resident Males & Their Responses*																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Type of prior experience—Courtship (C); Combat (F)	F	F	F	C	C	C	C	F	C	C	F	F	C	F	F	F	F	C	C	C
First test 30 minutes after above experience	F4	F4	F4	C4	C4	C4	C4	F3	C4	C4	F4	F4	C4	F4	F3	F4	F4	C4	C4	C4
Subsequent daily tests using drugged males in flasks as stimulus-animals	F1	F4	F3	C4	C4	C1	C4	F2	C4	C3	F4	N	C3	F4	N	F4	N	C4	N	C1
	F1	F4	N	C4	C3	N	C4	F2	C4	C3	F4	N	C4	F4	N	F4	N	C4	N	C1
	N	F1	N	C4	C3	N	C4	F2	C4	C3	F3	N	C3	F4	N	F3	N	C4	N	C2
	N	N	N	C4	C4	N	C4	F3	C4	C2	F1	N	C3	F4	N	F1	F1	C4	N	C1
	N	F1	F1	C4	C4	N	C4	F3	C4	C4	F4	N	C3	F4	C1	F3	F1	C4	N	C1
	N	N	N	C4	C4	N	C4	F3	C4	C4	F1	N	C3	F4	N	N	F1	C4	N	N
	N	N	N	C4	C3	N	C4	F3	C4	C3	N	N	N	F4	N	F1	F1	C4	N	N
	N	N	N	C4	C3	N	C4	F2	C4	C3	N	N	N	F4	N	F2	N	C4	N	N
				Stimulus-animals adrenalin-treated									Stimulus-animals anesthetized with MS-222							

* Same Resident Males as in Series I and II.

lus to courtship behavior in *Bathygobius* males was performed as follows: a resident male was selected which, on the basis of previous tests, showed a strong tendency toward courtship reactions; a gravid female was placed in a 50 ml. beaker filled with sea water for two minutes; the water from the beaker was then pipetted into the tank with the resident male. Within five to ten seconds, the male exploded into courtship. He displayed the courtship color phase and went into vigorous courting movements, swimming randomly all about the aquarium. If the running sea water supply to that tank was turned off, this courtship kept up for about an hour. If the sea water was kept running, however, the male lapsed into quiescence within 10 to 15 minutes.

In further testing the potency and site of origin of this stimulus, the resident males were all previously tested and given a strong courtship experience with a gravid female. This was to insure uniformity in their responses and, possibly, to increase their sensitivity toward these stimuli.

Obtaining the gravid-female-water as described above, it was found that as little as 0.5 ml. was effective in eliciting a courtship response. Smaller quantities produced either no response or a slight lightening of the male's coloration for a few seconds.

In order to determine the source of this stimulating factor, gravid females were wrapped closely in absorbent tissue paper. Care was taken that the tissue was not permitted to touch the anal-genital area. The females were first rinsed in a strong stream of sea water. Thus the tissue became soaked with the mucus secreted by the skin. In addition, small fragments of absorbent tissue paper (about 2-3 mm. square) were touched to the anus and to the tip of the urogenital papilla of gravid females. A small piece of the mucus-soaked tissue was dropped a few centimeters in front of a resident male. The other fragments of tissue were similarly tested.

Courtship responses were elicited only from the tissue that had been in contact with the urogenital papillae. The reactions of the males took place within 10 to 20 seconds and lasted for as long as 15 to 30 minutes. A full, vigorous courtship response was obtained. The mucus-soaked and anus-touched tissue fragments did not elicit a courtship response at any time, although in a few cases the male picked up the tissue in his mouth and spit it out as with a piece of food.

Various internal body fluids from gravid females were tested as possible sources of this chemical stimulus by either pipetting a few drops into the aquarium with a male, or by soaking the liquid up in a small bit of absorbent tissue paper and dropping the fragment near the resident.

The following fluids were tested: ovarian fluid; urine; coelomic fluid; blood; feces; stomach fluid. Of these, only the ovarian fluid elicited a courtship response. As little as 0.1 ml. in a five-gallon tank was sufficient to evoke a response lasting up to 30 minutes. The ovarian fluid was obtained by removing an ovary (enlarged and turgid with mature eggs), rinsing it off in 0.65 saline solution, cutting it open in a watch glass containing about 5 ml. of normal saline and squeezing out the eggs. After a few moments, the eggs settled to the bottom and the solution was pipetted off. Only a substance from the interior of the ovary was effective. Mucus and other fluids from males were negative in their effects.

It is not known whether this stimulating ovarian substance is secreted by the eggs or the ovary itself. Freshly extruded eggs are effective in eliciting courtship, but they lose the effectiveness within 10 or 15 minutes, whether or not they are fertilized. At the present time, no further data are available on the source and nature of the stimulating ovarian substance.

In order to determine the sensory organ involved in the response of males to this ovarian substance, the nostrils of the males were plugged by inserting a hot needle into each aperture (both incurrent and excurrent nostrils were plugged). The heat produced a plug of coagulated mucus at each aperture. This plug lasted for about two days. Permanently anosmic males were produced by cauterizing the entire nasal epithelium with a hot wire inserted into the nostrils.

These anosmic males did not respond to any amounts of the courtship-stimulating substance. The temporarily anosmic animals regained their sensitivity to the substance after two days, when the mucus plugs disappeared.

In comparing the efficacy of ovarian substance from animals at various stages in their ovarian cycle, the ovaries of non-gravid, recently spawned, pre-gravid and gravid females were used. Both the non-gravid and recently spawned females contained small, white, immature eggs. The ovaries of pre-gravid females (2-3 days prior to spawning) had eggs that could be extruded, but were not fertilizable. The latter ovaries elicited courtship responses in resident males, whereas the ovarian material from non-gravid and recently spawned females was only slightly effective or not at all. A slight reaction was one in which the male swam out of his shelter briefly, turning lighter as he did so.

It may be added that none of these ovarian substances had any perceptible effect on the behavior of isolated female gobies. Testicular material and male mucus secretions had no observable effect on either male or female behavior.

In connection with these experiments with chemical stimuli, a striking example of a conditioned response was observed in two of the resident males. In some of the preliminary tests, these two males were tested several times a day in their reactions to various fluids pipetted into their aquaria. After about a dozen tests, it became evident that they were responding with courtship behavior toward control substances, such as normal saline and sea water. It was further found that the simple act of holding an object or a hand a few inches above the tank was sufficient to elicit a courtship response. This conditioning was short-lived. After six to eight hours, the response to the conditioned stimulus was slight or absent, and the conditioning was no longer evident after 12 hours. In subsequent tests, intervals of at least 24 hours were allowed in order to avoid this complicating factor as much as possible.

Responses to Combination of Visual and Chemical Stimuli

On the basis of the results in test series I-III, resident males were classified into three reactive types:

A—Strong courtship reaction toward visual stimuli.

B—Frequent combat reactions toward visual stimuli.

C—Responses toward visual stimuli varied but never consistently strong; most frequent responses of the C1, F1 and N types.

Using resident males so classified, a series of tests were made in which the visual and olfactory stimuli were combined.

Type A Resident Males

An olfactory stimulus alone is sufficient to elicit a courtship response in these animals, but the addition of a visual stimulus of another goby in a flask orients the behavior. Without this visual stimulus, the courting behavior involves random movements all about the aquarium. With the visual stimulus, the male directs his attention toward the stimulus-animal, circling about the flask and butting against it. This courtship response continues for several hours, i.e. longer than with the olfactory stimulus alone. Furthermore, the courtship response is elicited and is continued toward all types of stimulus-animals: male or female, gravid or non-gravid, dark or light-colored, anesthetized or not, dead or alive, etc. The courtship continues even if the stimulus-animal exhibits combat behavior. The size limit of an adequate stimulus-animal is well below normal behavioral levels; a strong courtship will take place toward a 15 mm. goby in a flask (this was the smallest size available).

However, models and fishes of other species were ineffective in inducing an orientation of the courtship elicited by the olfactory stimulus.

Anosmic males, previously determined as highly reactive in terms of courtship response, never showed any courtship behavior. Their reaction toward gobies introduced into the aquarium was invariably a combat, even toward gravid females. Their responses toward a stimulus-animal in a flask were either of the combat or neutral type.

Type B Resident Males

The olfactory stimulus alone elicited a short courtship response in males. However, the combination of this with a visual stimulus of a goby in a flask usually produced a prolonged and vigorous courtship. In several cases, males so tested were found in subsequent tests to have changed to a type A reactivity.

In several tests, the visual stimulus was presented first, using a male as the stimulus-animal. A mutual combat began and was allowed to continue for a few minutes, then the ovarian fluid from a gravid female was poured into the tank. Within 10 or 15 seconds, the combat behavior of the male started to change to courtship, although the combat attempts of the stimulus-male continued for several minutes.

In a few cases, the resident males, when given a simultaneous olfactory stimulus and visual stimulus of a combating male, exhibited an alternation of combat behavior directed toward the stimulus-animal and of courtship behavior randomly oriented about the tank.

Type C Resident Males

An olfactory stimulus alone had little or no effect. Sometimes a brief lightening of the coloration took place and the male left his shelter, darted about the tank a few times, then returned to the shelter. In two cases, out of seven males tested, the olfactory stimulus alone elicited a strong courtship response. One of these two males subsequently changed to a type A reactivity.

A combined olfactory and visual stimulus elicited strong courtship responses and the resident males became highly responsive in that they then reacted with courtship toward visual and olfactory stimuli separately—i.e. type A reactivity. In a few cases, the courtship reaction toward the combined stimuli was temporarily changed to combat when the stimulus-animal exhibited darkening and sideward approach. In these cases, the courtship of the resident became random and disoriented, whereas spells of combat were distinctly oriented toward the stimulus-animal.

Sound Production

On the supposition that sound production might be involved in either the courtship or the combat behavior in *Bathygobius,* sound detection equipment of a preliminary nature was assembled. A waterproofed microphone was lowered into an aquarium containing the fish. The microphone was connected to a 10-watt amplifier, which, in turn fed the signal to the input of a tape recorder. The recordings were later played back into the aquarium with the same equipment, but using the microphone as a transducer.

The tape recordings were analyzed by means of oscilloscope observations, recording galvanometer traces and sound spectrograms. Unfortunately, the recording equipment was of low fidelity and the recordings contained some interfering background noise. The following descriptions of the sounds should be regarded as preliminary approximations.

In *Bathygobius,* only males were found to produce detectable sounds, and these were made only during the courtship behavior. No sounds could be detected during combat behavior between males. The courtship sounds consisted of short, low-pitched grunts, synchronized with the downward head-snapping or gasping movement which occurs frequently during vigorous courtship.

The intensity of these grunts could not be measured with the present equipment. The sounds were below audible level, even with the ear held up against the tank.

The frequency with which the sounds were produced was extremely varied. When the male was courting at some distance from the female, the grunts and head snaps occurred at the rate of only one or two during the course of a 30-second courting spell. When the male was vigorously courting a nearby female, or when the female was following the male into the nest, the grunts were produced at two- to four-second intervals, and sometimes four or five in quick succession.

The duration of each grunt varied from 0.15 to 0.20 of a second. Spectrograms of three sounds of about average duration are shown in Plate I. The fundamental pitch frequency of each grunt was a broad band from about 100 to 200 cycles per second. This value was determined from oscilloscope observations in which the fish sound was matched against sine waves of known frequency. The recording galvanometer showed a fundamental frequency at about 150 cps. Sound spectrograms in the 200 cycle/inch range showed a broad band about 100 cycles in width. The top of this band was at about 200 cps. at the beginning of the sound,

dropping to below 100 cps. toward the end. The resolution of the lower frequencies on the spectrogram was poor as a result of excessive low frequency noise in the recording.

Plate I shows that frequencies up to 4800 cps. were detected during the initial 0.05 second of the sound. Toward the end of the sound burst, the peak frequency dropped logarithmically. The pattern on the first 0.17 seconds of the spectrogram represents low frequency background noise in the recording.

When the sounds of a courting male were played back to an isolated gravid female, she began to dart quickly about the tank. Her swimming movements were similar to the short hops which are characteristic of a female that follows a courting male into the nest. After one or two minutes, she subsided into quiescence. This same behavior could be stimulated again but only if the playback were turned off for a half an hour or more. After three or four exposures to these stimulations, the gravid female no longer reacted to the sounds. Non-gravid females showed no discernable response to the sounds.

When the playback of the sounds was combined with the visual stimulus of another goby in a flask, the gravid female oriented some of her darting movements toward the stimulus-animal. A visual stimulus alone had no effect. Attempts to enhance the value of the visual stimulus by manipulating anesthetized, adrenalin-treated males into a simulation of the courting movements did not appear to increase the response of the female to the sounds, nor did models colored to mimic the light body and black chin of a courting male have an effect on orienting the response of a gravid female to the sound playback. There was no effect on the female's response by the addition of a chemical stimulus, i.e. water in which a male goby had been previously soaked.

The female's orientation toward a visual stimulus was unaffected by the relative position of the transducer. If the flask containing the stimulus-animal were moved, she followed it with short darts.

Isolated males responded to the playback of the courtship grunts. The male immediately swam up to the source of the sound, darted quickly about the tank and returned to the nest. He left his nest again and approached the transducer several times before he became quiescent. The same response was elicited 15 to 30 minutes later. After four or five trials with the same male, he no longer responded to the sounds. During the response, the male's coloration became a light tan (as in the courtship phase), but was unusual in that the chin and throat were almost white. If a visual stimulus of another goby

in a flask were provided at the same time or slightly after the playback began, the male approached the stimulus-animal, turned a dark color, and exhibited the movements typical of combat behavior.

Discussion

Visual Cues

In fishes, vision has always been considered a major factor in sex discriminatory and territorial behavior. Noble (1934) and Noble & Curtis (1939) reported that the coloration and behavior of an intruding animal are of prime importance in sex discrimination in sunfish and jewel fish *(Eupomotis* and *Hemichromis).* The size and shape of the stimulating object appear to function in the response of male guppies *(Lebistes)* toward females (Breder & Coates, 1935), while color plays a role in male-to-male encounters (Noble, 1938). Noble (1938) concluded that the bright colors of males of many teleost species function primarily as warning devices in territorial aggressions. The function of these colors in courtship behavior evolved subsequently. The work of ter Pelkwijk & Tinbergen (1937) and Baerends & Baerends-Van Roon (1950) on the stickleback *(Gasterosteus)* and the Cichlidae revealed that specific colors, patterns and shapes function as stimuli ("releasers") for particular actions on the part of both sexes during reproductive behavior. Tinbergen's interpretations (1951) of stickleback behavior have been applied in studies on *Cottus gobio* and *Gobius microps* by Morris (1954) and Nyman (1953), respectively. Extensive and rapid changes in color and pattern in *Bathygobius* are associated with environmental conditions (Tavolga, 1950), and the specific color phases that are associated with combat and courtship have been described earlier (Tavolga, 1954).

The behavior of the introduced animal is also important in determining the resident male goby's reaction (Tavolga, 1955a). A quickly retreating animal frequently elicits a nip-chase or combat response, whereas a slow retreat or none at all may stimulate courtship. Noble (1938) discussed a similar behavior among many species of fishes, and Baerends & Baerends-Van Roon (1950) describe the "submissive" behavior of females of many cichlids as one that stimulates courtship behavior. The general idea in most of these interpretations has been that initially the territory-holding male exhibits a generalized "challenge" to an intruder; then, a male intruder may return the "challenge" and a combat ensues. A fleeing intruder will be chased, whereas a gravid female holds her ground. The latter behavior stimulates courtship. This interpretation is inadequate for the be-

havior situation in *Bathygobius*, which appears to be more complex, as shown by some preliminary quantitative studies (Tavolga, 1955a). No distinctive colors or shapes serve to identify a female or her gonadal condition, yet a gravid female is courted vigorously regardless of her behavior, since the male is strongly stimulated by her ovarian secretions. The darkened coloration of a fighting male, together with the attendant fin-bristling, gaping, quivering and biting, form a visual stimulus-complex which elicits combat behavior on the part of the territory-holding male. Here there are two well-differentiated stimulus patterns which, in general, elicit a discriminatory response, i.e. courtship versus combat behavior, on the part of the resident male. The presence of intermediate and variable stimulus and response conditions deserves closer attention, however. Smaller males and non-gravid females react to the initial approach of a resident male in a variety of ways ranging from flight to quiescence. There is a tendency for the resident to court those individuals that hold their ground and to nip and chase those that flee, but the male's response is extremely variable (Tavolga, 1955a). The present work shows that the visual stimulus of the appearance and behavior of the intruder is only part of the configuration to which the resident responds. Low levels of olfactory stimulation as well as the recent experiences of the male contribute to the channeling of the response.

Olfactory Cues

The earlier work of Parker & Sheldon (1913) and Olmstead (1918) clearly separated olfactory sensitivity as distinct from the contact chemical sense of taste in fishes. More recently, the function of olfaction has been demonstrated in schooling (Wrede, 1932), fright reactions (von Frisch, 1941a and 1941b), and the detection and discrimination of plant odors (Walker & Hasler, 1949). There is ample evidence of a high level of sensitivity and discrimination of chemical stimuli present in the olfactory apparatus of many fishes. The role of olfaction in reproductive behavior is poorly known. Jaski (1939) postulated the existence of a hormone-like substance ("copulin") which is secreted by males of the guppy *(Lebistes)* and stimulates the receptivity of the female. However, both Jaski's evidence and interpretations could not be confirmed by Breder (as cited by Clark & Aronson, 1951). Chemical sense appears to be involved in sex discrimination in the catfish *(Ameiurus)* during courtship, and the "barbel-play" probably includes tactile and gustatory stimuli as well as olfactory (Breder, 1935; Hoagland, 1933). Chemical factors are clearly involved in the pair-

ing of the blind goby *(Typhlogobius)*, as described by MacGinitie (1939), but here too the chemical stimuli were not experimentally separated into olfactory and gustatory.

The nature of the stimulating substance in *Bathygobius* is not known, and the present evidence demonstrates only that it is rapidly diffusible and present exclusively in the ovaries and female genital tract. Whether it is secreted by the ovarian tissue or from the eggs, it is present in higher concentration or potency in ovaries with mature eggs. Ovaries of non-gravid or recently spawned females possess the courtship stimulating substance in small amounts or low potency.

The absence of courtship behavior in anosmic males demonstrates that the stimulus is an olfactory one rather than gustatory. Furthermore, the tendency toward combat behavior in these males may indicate that the olfactory stimulus not only elicits courtship but inhibits combat. This inhibition is not necessarily complete, as illustrated by the cases in which a conflicting situation was set up—an olfactory stimulus together with a visual stimulus of a male in combat. The actions of the resident then alternated from combat display toward the animal in the flask to random, non-oriented courtship.

Castrated male *Bathygobius* do not exhibit combat behavior. However, such operated males vigorously court gravid and non-gravid females, as well as other males in the same manner and to the same degree (Tavolga, 1955b). If, as demonstrated here, the courtship response is in the main elicited by an olfactory stimulus, it is possible that the male sex hormone affects the sensitivity of the olfactory organs in some way that renders these organs differentially sensitive to one or more substances. Castration may lower the sensitivity threshold and permit chemicals other than the ovarian fluid to stimulate courtship behavior.

Set

In an earlier study (Tavolga, 1955a), it was found that tests of responses by resident males had to be spaced several hours apart to avoid a persistence of the response from a previous test. In practice, a 24-hour spacing together with an alternation of sex of the test animal was found to be sufficient. This persistence may last for several days when the stimulus is purely visual and the stimulus-animal confined in a flask. It may be that the latter method is a more sensitive test for the existence of a predisposition on the part of the male, since the behavior of the stimulus-animal is restricted and plays less of a role in determining the response of the resident. The term *set* is one that is used

by psychologists for this type of predisposition or tendency towards a particular kind of response.

Series 1 of the visual tests indicated that a prior set of the male determined his type of response. This set was strong enough, in some cases, to overcome a visual stimulus towards another type of behavior. Specifically, a strong courtship orientation would overcome a visual combat stimulus, and courtship would continue. In cases where the combat display on the part of the stimulus-animal altered the response of the resident from courtship to combat, the set can be interpreted as weak. A set can also exist toward combat behavior, although this is never as strong as that toward courtship. Whether the neutral response of the resident indicates a third type of set or a lack of set, is a matter of nomenclature.

Series II showed that the appearance of the stimulus animals often has little effect upon the type of response if the resident is in a strong set. The only purely visual stimulus that can overcome a set is the color and behavior of another male in combat.

Series III showed that the set could be changed by a prolonged experience of either a vigorous courtship toward an unconfined gravid female or a mutual combat with another male. A courtship set, once established, was of longer duration than a combat set. Similarly, a courtship set was much easier to establish and harder to alter than a combat set.

The above method of establishing a courtship set included, of course, an olfactory stimulus. The olfactory stimulus is of prime importance, then, not only in stimulating courtship but in establishing the set. In situations of conflicting olfactory and visual stimuli, the courtship response usually predominated, although sometimes an alternating response occurred. In no case did the visual stimulus override the olfactory.

A male in courtship set will react with courtship toward the olfactory stimulus alone or toward a visual stimulus alone. The latter may even be subnormal in size.

A visual stimulus of a combating male can, at times, override a courtship set. The cues involved in a combat stimulus include not only a dark-colored adversary but the movements of sideward approach as well. A dark-colored but unmoving stimulus animal rarely elicits combat.

The possibility was considered that this apparent set could have resulted from the conditioning of the resident animals toward the act of presenting them with a stimulus situation. The type of stimulus-animal was varied as much as possible to prevent any conditioning, but the possibility exists nevertheless. The set, then, may be a situation induced by the testing procedure. Even so, the speed with which a set can be established, whether by conditioning or by some internal change, is of significance. Fishes are capable of forming remarkably rapid and complex associations. Topographic learning appears to be well-developed in many species (Goldsmith, 1905, 1912, 1914), and especially in littoral and tidal zone species such as *Bathygobius* (Aronson, 1951). Visual, tactile and kinesthetic factors are involved in maze-learning in fishes (Benuic, 1938; Churchill, 1916). Many investigators have used complex conditioning techniques in studies on visual perception (Herter, 1929; Perkins & Wheeler, 1930; Rowley, 1934). Hager (1938) showed that *Phoxinus* was capable of several types of associations simultaneously, and that retrained animals learn more quickly. Combinations of two or more sense modalities in the learning of configurations was demonstrated by Herter (1929) and Sanders (1940). The studies of Breder (1950, 1954) demonstrated the interdependence of visual and tactile senses among shelter-seeking fishes such as *Bathygobius* and *Pomacentrus*.

Fishes frequently form associations that may be surprising and unexpected. For example, males have "courted" a pipette or the observer's hand. A similar observation was made by Berghe (1929) during the course of his studies on the olfactory sense of *Cottus* and *Blennius*. Many home aquarists know how quickly their fishes learn to come to a specific feeding corner when the light is turned on, or the cover moved, or even when a shadow moves across the tank.

In the case described here, the response comprised a complete change to a courtship color phase and the courting movements for several minutes. Such a situation deserves further study, especially with a view toward finding out how quickly fishes learn to respond with specific behaviors toward models possessing elements of a normal stimulus pattern. On this basis, it could be possible to reinterpret the experimental evidence involving the reactions of fishes to specific stimuli, e.g. "sign stimuli" or "releasers," tested by means of abstracted models. The prespawning and spawning behavior in the stickleback (ter Pelkwijk & Tinbergen, 1937; Tinbergen & Van Iersel, 1947) was analyzed by this method, and the interpretation of the behavior as a series of sequentially dependant innate responses to releasing stimuli is extensively given by Tinbergen (1951). A similar line of thought is followed by Baerends & Baerends-Van Roon (1950) in their investigations of behavior in the Cichlidae. In all of this, and related, work, the innate nature of these responses

is assumed and there is little direct evidence given. Indeed, the very definition of an "innate behavior" as given by Tinbergen (1951) is subjective and intuitive. It is equally possible, therefore, that the responses of fishes, as well as of other vertebrates, to sign stimuli are conditioned or learned (in the broad sense of the word). Certainly fishes of many species can be quickly conditioned to respond to highly specific stimulus patterns, which can be purely artificial as well as being abstractions from their normal enviroment.

Sound Production

The production of sound by fishes is well-known, especially for groups such as the grunts (Haemulidae), and croakers and drumfishes (Sciaenidae). The early investigations of Agassiz (1850), Smith (1905) and Tower (1908) described various swim bladder mechanisms as the sound producing organs. Kellog (1953) summarized much of the literature available on noises made by marine organisms. There have been extensive studies, supported by the U. S. Navy and carried out by Fish (1954), wherein the sounds were analyzed as to frequency and intensity and the sound-producing species identified.

Some of the sounds made by marine fishes have accompanied feeding and schooling behavior, and some have been associated with spawning migrations, especially in the case of the "drumming" of croakers and drumfishes (Fish, Kelsey & Mowbray, 1952). The high frequency clicking in the sea horse (*Hippocampus*) may be involved in some phase of reproductive activity (Fish, 1953). The only specific case of sound production correlated with sexual behavior has been in the so-called croaking or purring gourami, *Trichopsis (Ctenops) vittatus,* as described by Stampehl (1931), Beyer (1931) and Reickel (1936). Both sexes in this species have been described as producing an audible purring noise during pre-spawning behavior.

In *Bathygobius,* the grunting noises produced by a courting male are distinctly stimulating to the female. Her response appears to be oriented by the visual stimulus. The olfactory and auditory stimuli comprise a set of distance cues leading toward successful pairing. The ovarian substance stimulates a non-oriented courtship behavior on the part of the male. This includes the production of sounds by the male. The sounds, in turn, stimulate generalized activity on the part of the female. The visual stimuli which occur subsequently, orient and re-enforce the pre-spawning behavior of both sexes. This,

however, cannot preclude the possibility that under other conditions, both the chemical and sound stimuli may also be of orienting and directional value. Observations in larger tanks and in the field will be necessary to determine the extent to which these fishes can orient themselves toward the source of a chemical or sound stimulus.

Although there has been a considerable amount of investigation on the auditory apparatus and function in fishes, the lowest frequency response limits have not been adequately established. The early work of Parker (1902, 1910, 1918) indicated that a number of fishes are sensitive to auditory stimuli at least as low as 100 cps. There is no evidence that the teleost ear may not be sensitive to even lower frequencies.

Rode (1929) and Dykgraaf (1933) performed some of the definitive experiments which showed the lateral line system of teleosts is sensitive to low frequency vibrations, including the detection of sharp blows, shocks and currents in the water. Rode (1929) obtained behavioral responses via lateral line stimulation with frequencies up to 60 cps. Schriever (1935, 1936) was able to detect action potentials from the lateral line nerve with stimuli of up to 150 cps. The uppermost reactive limit of the lateral line was placed at between 200 and 300 cps. with a tonal reproduction limit of 180 cps. (Suckling & Suckling, 1950).

On the basis of the above evidence, obtained from several species of teleosts, the fundamental frequency of the sounds produced by the male *Bathygobius* would fall into the reactive range of both the auditory and lateral line sensory systems, and at the present time it is not known which of the two senses, if not both, are involved in the reaction of the female. The lashing undulations of the body and tail of the male during courtship certainly produce oscillations that could be detected by the lateral line. These courtship undulations have been estimated as varying from five to twelve oscillations per second (Tavolga, 1954).

General Conclusions

It is evident that a number of sensory mechanisms function in concert to elicit, channel and modulate the responses of at least some fishes toward each other. Territorial and reproductive behavior is differentiated into its various forms by stimuli acting through the olfactory, auditory (including perhaps the lateral line system) and visual organs. Indeed, the visual cues involve a number of perceptual mechanisms such as discrimination of form, shade, color, movement, etc.

This interdependence of sense modalities has been widely studied in the higher vertebrates, including mammals, and the conclusions have been admirably stated by Beach (1951):

"Sexual arousal and mating behavior in all or nearly all animals appear to involve the activation of several different afferent systems. Orientation to, and movement toward a potential mate may occur in response to visual, auditory, or chemical cues. Any or all of these modalities may continue to influence the degree of excitment and to guide the bodily reactions of male and female during precoital courtship."

SUMMARY AND CONCLUSIONS

1. Males of *Bathygobius soporator* (Cuvier & Valenciennes) possess a highly differentiated territorial and pre-spawning behavior pattern. Sex discrimination is achieved by a differential response on the part of a resident male according to sex and gonadal condition of the intruding animal.

2. *Bathygobius* males respond readily to members of the same species, but do not react with either courtship or combat toward models and other fishes of similar shapes and sizes.

3. The courtship behavior of a male can be elicited by non-specific visual stimuli, i.e., differentiated sexually dimorphic cues are not present in this species. The appearance of another *Bathygobius* alone is often sufficient to elicit courtship, without regard to the behavior, coloration or sex of the stimulus-animal.

4. A distinct exception to the above is the reaction of a male to the appearance of a goby in combat, i.e. in cases where the stimulus-animal darkens and exhibits sideward approach. Visual stimuli comprising combat behavior are of primary value in eliciting a combat response on the part of a territory-holding male.

5. In the absence of a visually stimulating animal, the male responds with courtship to the presence of a chemical substance produced by a gravid female. The source of the stimulating material is the fluid of the ovary, and the male detects this rapidly diffusing substance by olfaction.

6. Males do not respond to visual stimuli in a stereotyped and predictable manner, and their type and intensity of response is governed, in part, by previous recent experiences. A strong predisposition (set) towards courtship response can be induced by a prolonged courtship experience. A similar, but less distinct, predisposition toward combat can also be induced. Repeated tests show that this predisposition can change from one type to the other, or toward a neutral responsiveness. Such changes are apparently "spontaneous" and cannot be correlated with changes in external conditions.

7. During courtship, the male produces frequent grunting sounds. Gravid females respond to these sounds with short quick darting movements, as would be characteristic of their pre-spawning behavior. The female's reactions to the sounds alone appear unoriented, but the presence of a visual stimulus of another goby serves to direct her movements.

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EXPLANATION OF THE PLATE

PLATE I

FIG. 1. Sound spectrogram of three bursts produced by a male *Bathygobius* during courtship. The low frequency trace at the beginning constitutes background noise and amplifier hum, and it is continuous throughout the recording.